

EVOLUTION OF THE GALIUM MULTIFLORUM COMPLEX
IN WESTERN NORTH AMERICA

I. DIPLOIDS AND POLYPLOIDS IN THIS DIOECIOUS GROUP

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The *Galium multiflorum* complex comprises a group of races which are spottily distributed through the interior of western North America. They occupy, for the most part, dry and rocky talus slopes and cliffs, and they range from the *Larrea* desert zone to alpine timberline. Life forms change correspondingly from low xerophytic desert shrubs to reduced alpine hemicryptophytes. All members of this racial complex are dioecious and sexually reproducing. Their mostly rotate, yellowish or greenish flowers are insect pollinated. Long silky hairs on the fruits facilitate wind dispersal.

The *Galium multiflorum* complex belongs to the section *Lopho-Galium* K. Schum. of this rubiaceous genus. Circumscription, differentiation, and first detailed taxonomic treatment along classical lines have been worked out by Ehrendorfer (1956). Further contributions, including a somewhat changed taxonomical evaluation, have been published by Dempster (1959).

Within the frame of a broad scientific project aiming at an understanding of the main evolutionary features of this world-wide genus along comparative lines (for publications available so far, see Ehrendorfer 1958), work on the *Galium multiflorum* complex has been continued and expanded since 1959. This has been made possible by financial support from a Rockefeller grant and especially from National Science Foundation grant number 9825. Under the guidance and extremely stimulating cooperation of Professor G. L. Stebbins, the author carried out intensive research work in 1959; this included study of habitats and accompanying vegetation for nearly all of the chief divisions of the *G. multiflorum* complex, collection of transplant material and extensive population samples for statistical analyses, cytological research, and comparison of practically all herbarium material available. Later this project was joined and continued by Lauramay T. Dempster, whose help in various respects is gratefully acknowledged.

The present research on the *Galium multiflorum* complex aims at a reconstruction of its evolution in time and space as part of the general unfolding of the Great Basin flora and vegetation since the Tertiary and at the demonstration of the main evolutionary mechanisms involved. Results will be published in a series under the general heading of which this is the first contribution. The main questions dealt with here are: (a) basic evolutionary mechanisms as elucidated by cytological behaviour; and (b) distribution of diploids and polyploids within the complex.

MATERIALS AND METHODS

Populations of various races of the *Galium multiflorum* complex studied in the field were designated by collection numbers. The italicized numbers in the text refer to the field collection numbers of the author and his various co-workers. Further data on these collections will be found in the detailed list of collections below. Transplant material was obtained and grown in the greenhouse of the Genetics Department, University of California, Davis, and later also in Orinda, California. Cultivation over long periods seems difficult, however, as requirements are quite specialized as to soil, temperature, etc. Carnoy solution (5 parts of 95 per cent alcohol: 3 parts of chloroform: 1 part of concentrated acetic acid) was used for the fixation of young flower buds in the field and of fresh shoot apices from transplanted material. Fixations were stored in the refrigerator. Saturated aceto-carmin with iron was employed for staining; anther material was squashed after short and gentle heating in the stain, whereas vegetative tissues were boiled in aceto-carmin for two minutes. A Zeiss standard Series GFL microscope was used for cytological work, and the drawings were made with a camera lucida. Herbarium vouchers from plants with known chromosome number will be deposited in principal herbaria after conclusion of the present research project.

GENERAL CYTOLOGY

Mitosis, meiosis and pollen grain mitosis were studied in various races of the *Galium multiflorum* complex. As a main result the existence can be established of a polyploid series with diploids, tetraploids and a local hexaploid (see discussion), all having the base number $x=11$. Apart from determination of chromosome numbers some general cytological observations have been made.

The dioecious sex differentiation in the group led to the question as to whether sex chromosomes were cytologically recognizable. Mitoses of shoot apices from male and female plants of the diploid *G. hallii* were carefully compared. No obvious difference in number or shape of chromosomes could be detected. One has to consider, though, that with relatively small and not very clearly differentiated chromosomes (fig. 1a), minor differences could easily escape notice. In various diploid and polyploid races meiosis in pollen mother cells were scrutinized in order to find heteromorphic bivalents of sex chromosomes, but without success. Cytological differentiation of males and females in the *G. multiflorum* complex, therefore, seems to be absent or cryptic.

Comparisons were made of mitoses from shoot apices of very distantly related diploids, like *G. hallii* and *G. hypotrichium* subsp. *tomentellum*, in order to find out whether structural differentiation of chromosome sets had occurred (fig. 1a, b). Results show that there is much similarity. Absolute size differences apparent from the figures 1a and 1b may be due to the developmental stage of the individual cells. In both races the chromosome set consists of: A) one pair of SAT-chromosomes,¹ B) one pair

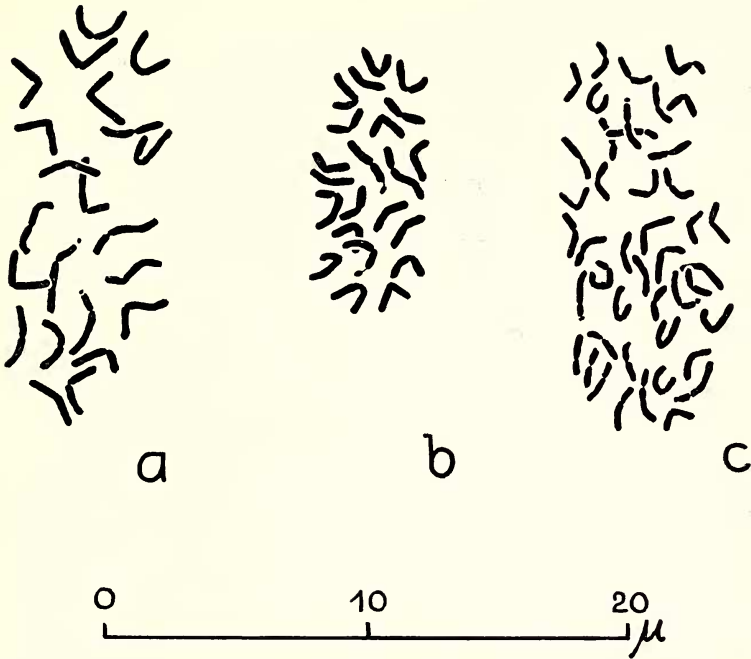


FIG. 1. Somatic mitosis in *Galium*. a, *G. hallii* (5901), b, *G. hypotrichium* subsp. *tomentellum* (5941), c, *G. grayanum* subsp. *glabrescens* (5963, tp. 2).

of long and strongly heterobrachial chromosomes, C) four pairs of chromosomes with less conspicuously different arms, and D) five pairs of chromosomes with median or submedian centromere. Groups C and D are not always clearly separable. This general pattern is also maintained in the allotetraploid *G. grayanum* subsp. *glabrescens* (fig. 1c). In spite of these similarities, indications for some structural differentiation can be found, e.g., in the SAT-chromosomes, where relation between long and short arms as well as satellite size are clearly different in *G. hallii* and *G. hypotrichium* subsp. *tomentellum*.

In spite of some cell-to-cell variability in chromosome size, there is a clear hereditary diminution of chromosome size with polyploidy. This is demonstrated better by comparison of somatic mitoses (fig. 1) from diploids than by comparison of corresponding stages of pollen meioses (fig. 2a, b) or pollen mitoses (fig. 2 l, m). Diminution of chromosome size is less obvious in the probably quite recent local hexaploid (fig. 2c). This reduction of chromosome size (and very likely nuclear size) in polyploids does not fully compensate the cell size increase correlated with

¹ The satellites often stick to the short arms, making it difficult to recognize the SAT-chromosomes. Such sticking seems to happen nearly always in pollen mitoses (fig. 2 l, m).

polyploidy, as is apparent from comparison of PMC's and young pollen grains which are larger in polyploids than in diploids (fig. 2a-c, l, m). Studies to determine the effect of polyploid level upon stomatal size are being carried on by Mrs. Dempster, with promising results for the use of stomatal measurement as an indication of ploidy when cytological evidence is lacking.

In polyploids of the *Galium multiflorum* complex there is occasional intra-individual somatic instability of chromosome number. This has been established for *G. grayanum* subsp. *glabrescens* (5963, tp. 1) and it probably occurs in *G. munzii* (5980, tp. c.). From excellent fixations resulting in exceptionally clear mitotic pictures, it is evident that the former plant has $2n=45$ as the most common number in young buds and shoot apices, but that occasional deviations occur, of which $-44 -43 -42 -41$ as a reductional series and -47 as an indication for accumulation were actually observed. One plant (5980, tp. c.) seems to vary between $2n=42 -44-45$. In a number of other polyploids, e.g., *G. grayanum* subsp. *glabrescens* (5963, tp. 2) and *G. munzii* var. *kingstonense* (5969), counts of numerous mitoses always gave the stable number $2n=44$. Intra-individual instability of chromosome number may be due to unbalanced primary number and/or spindle defects. Unstable somatic chromosome numbers have not been found in diploids.

Normal sexual reproduction is highly probable within the group. The course of pollen meiosis is remarkably normal in diploids and polyploids; male and female plants always coexist in the populations, often with an excess of males, and there is obvious morphological variability within the populations.

Chiasma frequency is variable. In the diploids with their relatively large chromosomes, frequency of bivalents with two chiasmata is often higher than 50 per cent, the other bivalents having only one chiasma (fig. 2d, e). Unpaired chromosomes seem to be extremely rare in the diploids. In the tetraploids with reduced chromosome size, the number of chiasmata is decidedly lower. In *G. hypotrichium* from Alpine County, for instance, there are only 15 per cent bivalents with two chiasmata in a plant from the Ebbetts Pass series (5920) and 10.9 per cent in a plant from the Sonora Pass series (5917) [each calculated from 50 PMC's]. Multivalents (trivalents with univalents and quadrivalents in chains and rings, fig. 2f) are relatively rare. In the above-mentioned plants there were 8 per cent PMC's with III+I and 28 per cent with IV (5920) and 8 per cent PMC's with III+I and 22 per cent with IV (5917). Univalents lag in anaphase I (fig. 2h), and are prematurely divided, but their halves are unable to divide a second time in anaphase II (fig. 2i); so they are eliminated or finally fuse with some of the telophase nuclei. As a result, pollen grains of polyploids occasionally contain deviating chromosome numbers (fig. 2m). This phenomenon must be basically responsible for some polymorphism of $2n$ numbers in populations of polyploids.

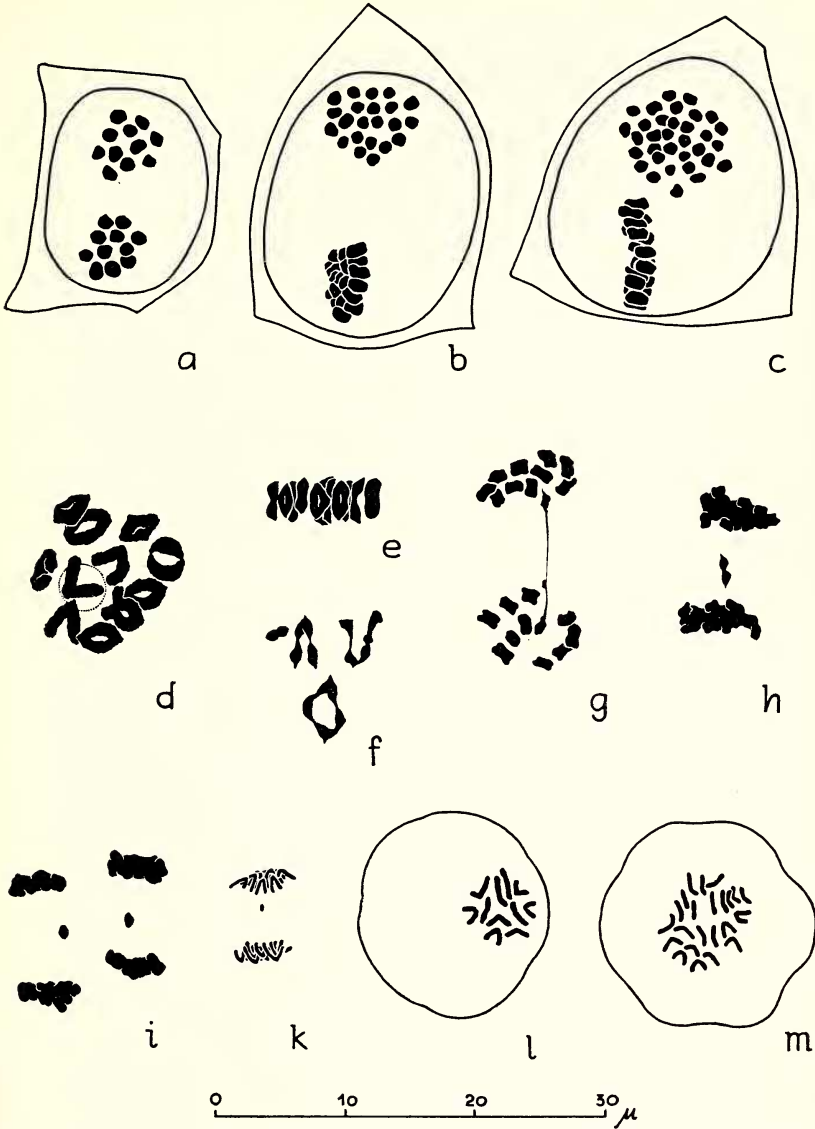


FIG. 2. Division figures in *Galium*. a-c, PMC metaphase II in diploid, tetraploid and hexaploid plants: a, *G. serpicum*-2x (5911-5913, fd. IIa); b, *G. munzii*-4x (5903, tp.); c, *Galium* (6x race), Warner Mountains (5909, 5910). d-i, PMC divisions: d, diakinesis, *G. grayanum*-2x (5933-5936); e, metaphase I, side view, *G. serpicum*-2x (5914); f, multivalents, III+I, IV chain, IV ring, *G. hypotrichium* subsp. *hypotrichium*-4x (5920); g, anaphase I with bridge and attached fragment, *G. parishii*-2x (5902); h, telophase I with lagging univalent, *G. hypotrichium* subsp. *hypotrichium*-4x (5917); i, telophase II with lagging univalent halves, *G. hypotrichium* subsp. *hypotrichium*-4x (5920). k-m, first pollen mitosis: k, anaphase with free acentric fragment, *G. hypotrichium* subsp. *hypotrichium*-2x (5916); l, metaphase *G. hypotrichium* subsp. *hypotrichium*-2x (5916); m, metaphase, aberrant pollen grain with $n=23$, *G. munzii* \times *G. hypotrichium* subsp. *subalpinum*-4x (5947).

In 3 diploids, 1 tetraploid and 1 hexaploid, consequences of chromosome aberrations have been seen: bridges with and without fragments in

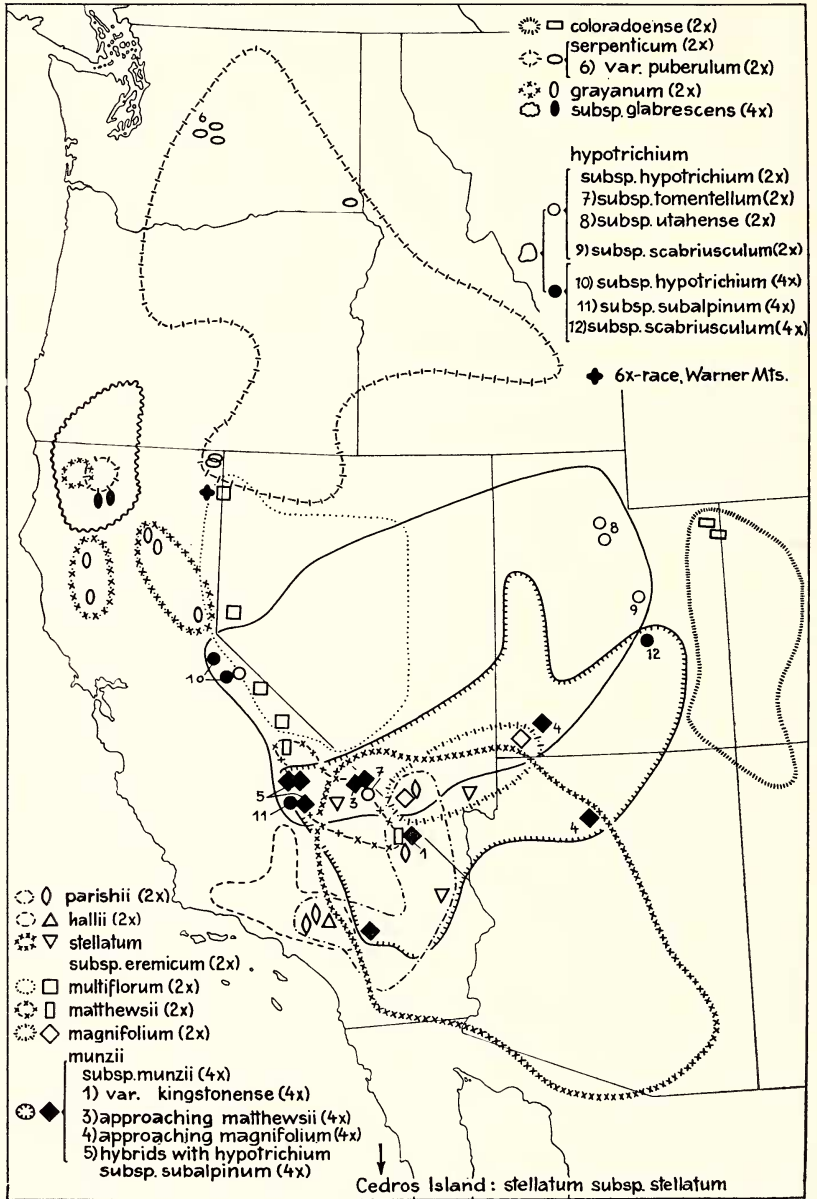


FIG. 3. Distribution of the *Galium multiflorum* complex, shown by outlines. Locations of populations examined cytologically are indicated by individual symbols.

anaphase I (fig. 2g), and liberation of attached fragments in anaphase of pollen mitosis (fig. 2k). In the hexaploid there are occasional spindle defects, restitution nuclei, and formation of resultant dyads.

Male sterility as a result of break-down of pollen development after normal meiosis has been observed in a diploid *G. serpenticum* plant from Mount Bidwell (5911).

DISTRIBUTION OF DIPLOIDS AND POLYPLLOIDS

Determination of chromosome numbers and ploidy levels is one of the major prerequisites for the reconstruction of the evolutionary history of the *Galium multiflorum* complex. So far, chromosome counts are available for most of the major species, subspecies, and hybrid populations presently recognized. These counts originate from 51 populations and more than 100 individuals. Populations with known chromosome numbers are shown on the map (fig. 3), as single symbols within the outlines of the total distributional area of their respective taxa.

The following list contains further information on geographical origin and habitat of the populations cytologically studied. The abbreviation "fd." indicates fixations made in the field, mostly comprising several individuals; chromosome counts in such instances usually refer to more than one individual. The abbreviation "tp." indicates fixations from single transplant individuals further designated by numbers or letters. Definite chromosome numbers are given after a minimum of several unquestionable counts per plant; if only one or few counts are available the symbol " \pm " is used. The abbreviation "ca." refers to approximate counts. Chromosome numbers are indicated in the diploid state ($2n$). They have been determined from vegetative tissues in flowers and shoot apices. Where counts have been carried out on pollen meiosis or pollen mitosis, $2n$ numbers have been extrapolated and an asterisk is added.

As is evident from the list, diploid populations are always uniform in respect to chromosome number ($2n=22$), while certain fluctuations of $2n$ numbers around straight x multiples have been observed in some polyploid populations: *G. munzii* from Wildrose Canyon ($2n=44, 46$), Lone Pine Creek ($2n=42, 44$), Zion National Park ($2n=44, 45$) and Grand Canyon ($2n=42, 44$). Polyploids are obviously less sensitive to aneuploidy, addition or loss of chromosomes, than diploids. The origin of aberrant types must be due to meiotic irregularities and deviating chromosome numbers in the gametes, or to intra-individual somatic instability, with similar consequences, situations which have already been referred to.

In the following list of collections, only previously published names have been used, and the taxonomic scheme followed is not necessarily in entire agreement with the author's present views. The taxonomic position of the plants in some of the populations represented is still uncertain, and their placement in the list is conservatively based on published work of the past

GALIUM COLORADOENSE Wight

Utah, Dinosaur National Monument, 1 mile west of campground near Split Mountain, 5150 feet; Shinarump Quartz conglomerate; sandy and gravelly north slope, very open Pinyon-Juniper: *Ehrendorfer & Stutz 5950*. tp.: 2n=22

Utah, Uintah County, just south of Brush Creek on Highway 44, ca. 11 miles north northeast of Vernal, ca. 6000 feet; open bushy and herbaceous pioneer growth on steep Jurassic sandstone cliff: *Ehrendorfer & Stutz 5951*. tp.: 2n=22

GALIUM GRAYANUM Ehrendf.

subsp. GRAYANUM

California, Tehama County, North Coast Ranges, South Yollo Bolly Mountain, 7700-8080 feet; gentle to steep talus slopes, metamorphic schists; subalpine pioneer vegetation among very open *Abies magnifica*: *Ehrendorfer 5933, 5934, 5935, 5936*. fd.: 2n=22*

California, Lake-Colusa County, Goat Mountain, North Coast Ranges, 6000 feet: leg. *G. L. Stebbins* fd.: 2n=22

California, Lassen National Park, Brokeoff Mountain, 9000 feet; gentle to steep talus slopes, volcanic andesite; subalpine pioneer vegetation: *Ehrendorfer, Stebbins & Dempster 5964, 5965, 5966, 5967*. tp. 0 : 2n=22

tp. 1 : 2n=22

California, Butte-Plumas County, Summit above Jonesville, ridge east of pass, 6700-7000 feet; rocks and talus slopes, volcanic andesite; pioneer vegetation among subalpine chaparral, *Abies magnifica* and *Pinus monticola*: type locality, *Ehrendorfer 5937, 5938, 5939*. fd.: 2n=22*

California, Placer County, Sierra Nevada, Sugar Bowl resort southwest of Donner Summit, 7200 feet; steep northeast slope, andesite talus and rocky outcrops; pioneer vegetation among *Quercus vaccinifolia*, *Abies magnifica* and *Pinus monticola*: *Ehrendorfer & Stebbins 5905*. fd.: 2n=22*

subsp. GLABRESCENS Ehrendf.

California, Siskiyou-Trinity County, west flank of Scott Mountain, ca. 6300 feet; ultrabasic intrusives; serpentine-peridotite; talus and gravel within very open *Pinus jeffreyi* and *Abies concolor*: *Ehrendorfer & Stebbins 5915*. fd.: 2n=44*

California, Siskiyou County, 0.5 mile south-southeast of Castle Lake, southwest of Mount Shasta village, ca. 6000 feet; serpentine talus, pioneer vegetation among *Arctostaphylos nevadensis*, *Pinus monticola*, *Abies magnifica*: type locality, *Ehrendorfer, Stebbins & Dempster 5963*. tp. 1 : 2n=41-42-43-44-45-47

tp. 2 : 2n=44 (stable)

GALIUM HALLII Munz & Jtn.

California, Los Angeles County, northeast side of San Gabriel Mountains, Sawmill Canyon at west end of Swartout Valley, between Wrightwood and Lone Pine, 6600 feet; on steep north slopes, in mineral soil (schist) among *Quercus Kelloggii* and *Pinus ponderosa*: *Ehrendorfer 5901*. fd.: 2n=22

GALIUM HYPOTRICHIMUM Gray

subsp. HYPOTRICHIMUM

California, Alpine-Mono County, Sierra Nevada, ca. 0.5 mile south of Sonora Pass, ca. 10,200 feet; wind-exposed talus slope on crest line, volcanic rocks; very scattered pioneers: type locality, *Ehrendorfer 5916*. fd.: 2n=22*

fd.: 2n=22

California, Alpine County, Sierra Nevada, ca. 2 miles west of Sonora Pass, ca. 9500 feet; sheltered west slope, volcanic talus; *Ribes* bushes and herbs: *Ehrendorfer 5917*. fd.: 2n=44*

California, Alpine County, Sierra Nevada, ca. 0.5 mile southeast of Ebbetts Pass, 8950 feet; northwest slope, volcanic talus; *Symphoricarpos*, *Artemisia*, herbs: *Ehrendorfer 5920*. fd.: 2n=44*

subsp. SCABRIUSCULUM Ehrendf. (*G. coloradoense* var. *scabriusculum* Dempster)
Utah, Carbon County, Castle Gate, side canyon on southwest of main valley, entrance ca. 1 mile northwest of the town, ca. 6500 feet; gully with steep sandstone slopes; grassy and herbaceous cover among open *Pinus ponderosa* and *Symphoricarpos*: Ehrendorfer & Stutz 5954. tp.: 2n=22

Utah, Emery County, small side canyons on either side of Buckhorn Wash, ca. 1 mile north of San Rafael River bridge, ca. 4500 feet; dry bottom of gullies with boulders and sand from sandstone; very open Pinyon-Juniper and scrub: near type locality, Ehrendorfer & Stutz 5952, 5953. tp. a: 2n=44
tp. b: 2n=±44
tp. c: 2n=ca. 44

subsp. SUBALPINUM (Hilend & Howell) Ehrendf.
California, Inyo County, Sierra Nevada, Cottonwood Lake Basin, slopes north and northwest above Muir Lake, ca. 11,200 feet; granitic talus; open *Pinus balfouriana*, *Holodiscus* and pioneer herbs: Ehrendorfer 5945, 5946. tp. 1: 2n=±44
tp. 2: 2n=±44

subsp. TOMENTELLUM Ehrendf.
California, Inyo County, Panamint Mountains, Telescope Peak, below top on north side, ca. 11,000 feet; talus of metamorphic schists; pioneers among very open *Pinus aristata*: type locality, Ehrendorfer 5941. fd.: 2n=22

subsp. UTAHENSE Ehrendf.
Utah, Utah County, Wasatch Mountains, American Fork Canyon, steep north slopes along trail to Timpanogos Cave, 6400-6800 feet; limestone rocks and talus; bushes and herbaceous pioneers among scattered *Pseudotsuga* and *Abies*: type locality, Ehrendorfer & Stutz 5949. tp.: 2n=22

Utah, Salt Lake County, Wasatch Mountains, steep north slopes, ca. 1 mile southwest of Alta, ca. 9000 feet; limestone rocks and crevices; vegetation similar to 5949; Ehrendorfer & Stutz 5955. tp.: 2n=22

GALIUM MAGNIFOLIUM (Dempster) Dempster
Nevada, Clark County, Charleston Mountains, southwest of Las Vegas, near Cottonwood Springs, canyon above Bar Nothing Ranch (= Wilson's Ranch), ca. 4200 feet; steep north slope along creek, alluvial material below mesozoic sandstone; open Pinyon with *Artemisia*, *Yucca* and *Opuntia*: type locality, Ehrendorfer & Dempster 5975. fd.: 2n=±22
tp.: 2n= 22

Utah, Washington County, ca. 1 mile northeast of Hurricane, steep slope above tributary of Virgin River, ca. 3000 feet; Jurassic sandstone and talus; with *Ephedra*, *Artemisia*, etc.; Ehrendorfer & Dempster 5979. fd.: 2n=22

GALIUM MATTHEWSII Gray
California, Inyo County, east side of Sierra Nevada, Big Pine Creek, slopes above the camp site and road head, 8800 feet; loose granitic talus and sand, among *Artemisia*: Ehrendorfer 5922. fd.: 2n=22*

California, San Bernardino County, Kingston Mountains, steep slopes south of Kingston Pass, ca. 5500 feet; crevices of granite: Ehrendorfer & Dempster 5974. tp. a: 2n=22
tp. b: 2n=22

GALIUM MULTIFLORUM Kell.
California, Modoc County, south of Eagleville, cliff above Lower Alkali Lake, 5000 feet; in crevices and at the base of east-northeast-exposed basalt rocks: Ehrendorfer & Stebbins 5908. tp.: 2n=22

California, Mono County, northwest shore of Mono Lake, on upper terrace, 6550 feet; among *Artemisia* and *Purshia* on light pumice sand: Ehrendorfer 5918. tp.: 2n=22

Nevada, Storey County, Washoe Mountains, 2.2 miles north of Virginia City on Highway 17 to Reno, ca. 6600 feet; steep north slope, on volcanic talus among *Artemisia*, open Pinyon-Juniper along gully: type locality, *Ehrendorfer & Stebbins* 5906. fd.: 2n=22*

forma *HIRSUTUM* (A. Gray) Ehrendf.

California, Mono County, Sherwin Grade, dry wash southwest of Highway 6, ca. 6600 feet; volcanic rhyolite talus and rocks among *Artemisia*, open Pinyon: *Ehrendorfer & Dempster* 5921. tp.: 2n=22

GALIUM MUNZII Hilend & Howell

var. *KINGSTONENSE* Dempster

California, San Bernardino County, Kingston Mountains, steep slopes south of Kingston Pass, in gullies and toward the top, 5800-6000 feet; rocky ravines and steep slopes with Pinyon, granite: type locality, *Ehrendorfer & Dempster* 5969, 5971.

tp. a: 2n=44

tp. b: 2n=44

subsp. *MUNZII*

California, Inyo County, Lone Pine Creek just above its break-through into Owens Valley, ca. 5000 feet; steep north slopes with Pinyon on granitic sand: *Ehrendorfer* 5927.

tp. a (glabrous form): 2n=42

tp. b (hirsute form): 2n=44

California. Inyo County, Panamint Mountains, Wildrose Canyon, above charcoal kilns, ca. 7200 feet; metamorphic schists and sandstones; open Pinyon and Juniper, talus: *Ehrendorfer & Dempster* 5968.

tp. a (hirsute form): 2n=44

tp. b (hirsute form): 2n=44

tp. c (glabrescent form): 2n= ca. 44

tp. d (approaching *G. mathewsii*
= var. *carneum* Hilend & Howell, 1934): 2n=46

California, Inyo County, Panamint Mountains, along trail from Mahogany Flat to Telescope Peak, ca. 8500 feet; metamorphic schists; talus, with *Holodiscus*, *Artemisia*, etc.: *Ehrendorfer* 5943. fd.: 2n=44*

California, San Bernardino County, San Bernardino Mountains, lower portion of Cushenbury Canyon, ca. 5000 feet; granitic talus, northeast slopes just above the wash, among open Pinyon-Juniper: *Ehrendorfer* 5903. fd.: 2n=±44

tp.: 2n=44*

probable hybrids with *G. HYPOTRICHUM* subsp. *SUBALPINUM*

California, Inyo County, east side of Sierra Nevada, Lone Pine Creek, 0.5 mile below Whitney Portal, steep ravine with northwest exposure, ca. 8370 feet; granitic boulders and talus; open *Chrysothamnus* and *Artemisia*: *Ehrendorfer* 5929. fd.: 2n=44*

tp.: 2n=±44

California, Inyo County, east side of Sierra Nevada, Little Cottonwood Creek above Lone Pine, ca. 8800 feet; granitic rock and sand; *Cercocarpus*, *Holodiscus* and *Artemisia*: *Ehrendorfer* 5947. fd.: 2n=44*

approaching *G. MAGNIFOLIUM*

Utah, Zion National Park, trail to The Narrows, ca. 4300 feet; sandy and gravelly talus below Navajo sandstone cliffs, eastern exposure; loose cover of herbs and scrub; *Ehrendorfer & Dempster* 5980.

tp. a (hirsute form): 2n=44

tp. b (hirsute form): 2n=45

tp. c (glabrous form): 2n=±42-44-45

Arizona, Grand Canyon National Park, south rim, uppermost portion of Grand View

Trail, ca. 7000 feet; arenaceous limestone; steep slope with herbs, among *Cercocarpus*, *Amelanchier* and *Pinus edulis* in northern exposure: *Ehrendorfer & Dempster 5981*.

tp. a (somewhat hairy form): $2n=44$

tp. b (glabrous form): $2n=42$

GALIUM PARISHII Hilend & Howell

California, San Bernardino County, San Bernardino Mountains, top of San Gorgonio Mountain, 11,485 feet: leg. *P. Raven 11,152*. fd.: $2n=22^*$

California, Los Angeles County, San Gabriel Mountains, hills about 2 miles north of Big Pines, ca. 6500 feet; granitic talus in northwest exposure: open *Artemisia* with *Pinus jeffryi*: *Ehrendorfer & Grant 5902*. fd.: $2n=22^*$

California, San Bernardino County, Kingston Mountains, steep slopes south of Kingston Pass, ca. 5600 feet; granitic talus slopes and shady rock crevices: *Ehrendorfer & Dempster 5972, 5973*. fd.: $2n=22$
tp.: $2n=22$

Nevada, Clark County, Charleston Mountains, Kyle Canyon, southwest slopes, southeast of Cathedral Rock camp site, ca. 7600 feet; limestone talus and rock crevices among open *Pinus*, *Abies* and *Cercocarpus*: *Ehrendorfer & Dempster 5976*.
tp.: $2n=22$

GALIUM SERPENTICUM Dempster [*G. watsonii* (Gray) Heller sensu Ehrendf.]

Washington, Asotin County, Blue Mountains, below the crest overlooking Indian Tom Creek, 30 miles southwest of Asotin, ca. 5300 feet; basalt, rocks and fine talus below, open bushy and herbaceous pioneer growth: *Ehrendorfer & Ownbey 5956, 5957*.
tp. 1: $2n=22$

California, Modoc County, Warner Mountains, Mount Bidwell, southeast side of plateau top, ca. 8000 feet; basalt talus; bushy and herbaceous pioneer vegetation with *Artemisia*, grasses, etc.: *Ehrendorfer & Stebbins 5911, 5912, 5913*.

tp. I: $2n=22$

$2n=22^*$

tp. II-1: $2n=22$

fd. II: $2n=22^*$

California, Modoc County, Mount Bidwell, southwest side of plateau top, below rim, ca. 7600 feet; east slope, steep basaltic talus; similar vegetation: *Ehrendorfer & Stebbins 5914*. fd.: $2n=22^*$

var. *PUBERULUM* (Piper) Dempster [*G. watsonii* (Gray) Heller subsp. *puberulum* Ehrendf.]

Washington, Kittitas County, Wenatchee Mountains, west-southwest slope in upper Beverley Creek, ca. 4500 feet; serpentine rock and talus, open pioneer vegetation: *Ehrendorfer & Kruckeberg 5958, 5959*. fd.: $2n=22^*$
tp. 1: $2n=22$

Washington, Kittitas County, Liberty, knoll above Boulder Creek, ca. 3500 feet; Eocene sandstone shale; sandy talus slope with pioneers: *Ehrendorfer & Kruckeberg 5960*.
tp. 1: $2n=22$

Washington, Kittitas-Chelan County, south slope near Blewett Pass, ca. 4000 feet; sandy talus: *Ehrendorfer & Kruckeberg 5962*.
tp. 1: $2n=22$

GALIUM STELLATUM Kell. subsp. *EREMICUM* (Hilend & Howell) Ehrendf.

California, Inyo County, Darwin Falls, about 3 miles south of Lone Pine-Death Valley highway, 3000 feet; rock crevices in canyon walls, metamorphic schists; desert scrub and some cacti: *Ehrendorfer & Dempster 5940*. fd.: $2n=22$

California, San Bernardino County, hills south of Highway 66, 7 miles northeast of Essex, ca. 1000 feet; steep rocky slope, gneiss; desert scrub (*Larrea*, etc.): *Ehrendorfer & Dempster 5982*.
tp.: $2n=22$

Nevada, Clark County, Valley of Fire State Park, east entrance opposite Elephant Rock, ca. 2000 feet; rocky north slope, Triassic sandstone; desert scrub: *Ehrendorfer & Dempster 5978*. tp.: $2n=22$

UNNAMED TAXON (6x race)

California, Modoc County, Warner Mountains, Horse Mountain, south of and toward summit, ca. 8500 feet; basalt talus and rocks; grassy and shrubby pioneers: *Ehrendorfer & Stebbins 5909, 5910*. fd.: $2n=66^*$

GALIUM ROTHROCKII Gray subsp. *ROTHROCKII* (a monoecious member of section *Lopho-Galium*, not directly connected with the *G. multiflorum* complex).

Arizona, Grand Canyon National Park, south rim, uppermost portion of Grand View Trail, ca. 7000 feet; arenaceous limestone; steep slope with herbs, among *Cercocarpus*, *Amelanchier*, and *Pinus edulis* in northern exposure (together with *G. munzii* approaching *G. magnifolium*); *Ehrendorfer & Dempster 5981A*. tp.: $2n=22$

DISCUSSION

In spite of general dioecious sex differentiation, an eu-polyploid series $2x-4x-6x$ with $x=11$ has developed in the *Galium multiflorum* complex, just as in practically all of the hermaphrodite groups of this genus which have been checked cytologically so far. Polyploidization is less advanced than in some other groups with the majority of the races still diploid and only one very local hexaploid known. In the European section *Lepto-Galium*, for instance, polyploidization has proceeded to the $10x$ level, with the most widely spread and successful types (*G. pumilum*, *G. rubrum*, *G. marchandii*) on the $8x$ level (Ehrendorfer 1954).

Sexual differentiation in the *G. multiflorum* complex exemplifies an evolutionary trend established in a number of other New World groups of the genus as well. No sex chromosomes have been recognized so far. Sex differentiation in the complex must be similar in character to that in *Rumex* subgenus *Acetosella* or *Melandrium* (Löve and Sarkar 1956, and literature cited there). In these groups genetic sex determiners for the heterogametic sex are so strongly epistatic that polyploidization does not upset the 1:1 segregation mechanism ($XY = \sigma$, $XXXXY = \sigma$, $XXXXXY = \sigma$).

The basic evolutionary differentiation of the *G. multiflorum* complex is accompanied by only very slight visible structural changes in chromosomes. Occasional spontaneous aberrations give a clue as to the origin of these.

As a result of the total evolutionary differentiation within this species complex, "marginal" and "extreme" positions in respect to distribution, ecology, and morphology are taken by diploids. Known sympatric contacts between diploids are rare. *Galium matthewsii* and *G. parishii* grow in mixed populations in the Kingston Mountains of southeastern California, but there are no indications of hybridization. This must be owing to the development of internal barriers, possibly involving chromosome structure. In contrast with the diploids, the polyploids are intermediate in distribution, ecology, and many morphological characters. There is some additional evidence that they are of hybrid origin and hybridize

much more freely with each other than do the diploids (e.g., *G. munzii* and *G. hypotrichium* subsp. *subalpinum* on the eastern slope of the southern Sierra Nevada). The present cytological findings substantiate the hypothetical racial diagram and interpretation developed by the author in 1956 (fig. 7): therein the polyploid *G. grayanum* subsp. *glabrescens*, *G. munzii*, and the partly polyploid *G. hypotrichium* form central "hot spots" of the complex, while all the marginal racial "cornerstones" are diploid. The general evolutionary situation therefore is very similar to that in other *Galium* groups, e.g. the section *Lepto-Galium* (Ehrendorfer 1954, 1955).

Details of cytological behaviour of the polyploid members of the *G. multiflorum* complex are very much in conformity with facts already known from European species: diminution of chromosome size in polyploid, stabilization of chromosome pairing, possibly via some influence on chiasma frequency, occasional irregularities of chromosome distribution into the gametes caused by formation of multi- and univalents and consequent appearance of biotypes with aberrant chromosome numbers. Intra-individual somatic instability of chromosome number has not been reported for *Galium* before, but the phenomenon seems not to be rare in polyploids (Gottschalk 1958, and literature cited there).

The cytological data here set forth point the way to some revisions in the taxonomic treatment of the *G. multiflorum* complex. The tetraploid *Galium grayanum* subsp. *glabrescens*, for example, should perhaps be accorded specific status, but in other cases specific separation on the basis of different ploidy levels seems impossible and highly impractical as within *G. hypotrichium* where even subspecific separation of the very closely adjacent and very similar 2x and 4x populations on Sonora Pass (Sierra Nevada) is an extreme procedure. Obviously no generalized rules can be applied in diploid-polyploid racial pairs, as has been previously shown with European *Lepto-Galium* and other groups. Taxonomic questions concerning the *Galium multiflorum* complex will be dealt with in other papers of this series.

SUMMARY

1. The western North American *Galium multiflorum* complex consists of sexual, dioecious races. Chromosome numbers have been established for most of the recognized taxa, including counts from 51 populations and more than 100 individuals. Primarily the chromosome numbers form an eu-ployploid series $2x-4x-6x$ with $x=11$. The distribution of the various diploids and polyploids is mapped.

2. Cell size (PMC's, pollen) is generally increased in polyploids.

3. Chromosome size and number of chiasmata are generally reduced in polyploids.

4. In two tetraploid plants a certain intra-individual somatic instability of chromosome number has been established; this has not been observed in diploids.

5. In polyploids there is a limited amount of multi- and univalent formation during PMC meiosis, with consequent irregularities of chromosome number in the gametes.

6. In four tetraploid (but never in diploid) populations, individuals with different standard chromosome numbers ($2n=42-44-45-46$) have been observed.

7. No differences in the chromosome sets of male and female plants could be demonstrated.

8. In PMC meioses and pollen mitoses some consequences of spontaneous chromosome aberrations (bridges, fragments) have been found.

9. Chromosome sets of various diploids and polyploids are quite similar, but there are certain differences (e.g. in the SAT-chromosomes) as a result of structural changes.

10. Cytological findings are briefly discussed from comparative evolutionary and taxonomic viewpoints.

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A NEW SPECIES OF LYCIUM IN NEVADA

CORNELIUS H. MULLER

A unique endemic *Lycium* occurs in Nevada in the area of the Atomic Energy Commission Nevada Test Site on Frenchman Flat. The plant was first discovered by Dr. William H. Rickard who remarked its extremely viscid, 4-merous corolla, and who suspected that it represented an undescribed species. It was collected in quantity by him, V. K. Carpenter, and Janice E. Beatley in the course of ecological investigations and subsequently by Dr. Beatley at my request. Material was submitted almost